The number of species in the wattle-eye genus Dyaphorophyia

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Le nombre d'espèces dans le genre *Dyaphorophyia*. Les pririts (ou gobemouches caronculés) du genre *Dyaphorophyia* sont considérés comme appartenant à quatre ou six espèces. Cette différence est due au fait que les taxons *blissetti*, *chalybea* et *jamesoni* sont traités soit comme une seule espèce comprenant trois sous-espèces, soit comme trois espèces à part entière. L'auteur analyse les arguments en faveur (principalement les différences morphologiques et la parapatrie altitudinale de deux des taxons) et en défaveur (leurs plumages juvéniles similaires, la variation individuelle des vocalisations et le niveau comparable des différences morphologiques entre les sous-espèces d'une espèce proche) de chaque traitement, et suggère que, pour le moment, il est préférable de ne reconnaître qu'une seule espèce, malgré les arguments pour l'attribution du statut d'allo-espèce à chaque taxon.

Summary. The wattle-eyes in the genus *Dyaphorophyia* are considered to comprise either four or six species. This difference is due to the treatment of the taxa *blissetti*, *chalybea* and *jamesoni*, which are variously considered to be a single species comprising three subspecies, or three separate species. This paper discusses the arguments pro (principally the morphological differences and elevational parapatry of two taxa) and contra specific status (their similar juvenile plumages, individual variation in vocalisations and the similar level of morphological differences exhibited amongst subspecies of a closely related species), and suggests that, for now, it is preferable to recognise just one species, despite the arguments in favour of recognising all three taxa as allospecies.

The wattle-eyes in the genus *Dyaphorophyia* are considered to comprise four species in *The Birds of Africa* (Urban *et al.* 1997), whereas in some other recent works (Dowsett & Dowsett-Lemaire 1993, Dickinson 2003) six species are listed. The difference lies in the treatment of the taxa *blissetti*, *chalybea* and *jamesoni*, which are variously considered to comprise a single species comprising three subspecies, or three separate species. Here I discuss the arguments pro and contra these treatments.

No molecular analysis of this group is presently available and no proof of sympatric occurrence during the breeding season (suggesting separate species) or evidence of interbreeding in contact zones (suggesting conspecificity) exists. It should also be noted that molecular studies do not always produce unambiguous results (see Maclean *et al.* 2005 for a recent overview). To establish which taxa in this group of related populations should be considered as species, one therefore must resort to the comparison and evaluation of the differences in morphology, acoustics, behaviour, habitat, etc., and the evaluation of the level of resemblance in related groups.

The genus Dyaphorophyia

The genus Dyaphorophyia, which is sometimes subsumed within Platysteira, forms part of the family Platysteiridae, which further includes the genera Megabyas, Bias, Pseudobias (all three monotypic), Batis (19 species) and Platysteira (4 species) (Louette 2006). The family is endemic to sub-Saharan Africa, with one monotypic genus (Pseudobias) endemic to eastern Madagascar. In their compilation of molecular analyses of oscine passerines, Jønsson & Fjeldså (2006) place these genera in the 'Crown Corvida clade 7', together with several other Australasian and Malagasy genera as well as African helmet-shrikes and bushshrikes. Other than the taxa blissetti, chalybea and jamesoni, the genus Dyaphorophyia comprises three incontrovertible species: the colourful Yellow-bellied Wattle-eye D. concreta and the classically coloured and rather similar Chestnut D. castanea and White-spotted Wattle-eyes D. tonsa. All are small, very short-tailed, insectivorous forest birds with conspicuous blue, purplish or green eye-wattles. All populations of each species have very similar measurements (see Louette 2006), and eye-wattles are present in both sexes, but undeveloped in immatures.

The Yellow-bellied Wattle-eye D. concreta has a very disjunct distribution and four subspecies (Figs. 1-2). Both morphological variation and sexual dimorphism are important and regionally variable, with unusual characteristics in plumage coloration, resulting in morphologically feminine males, semi-feminine males and hyper-feminine females (Louette 2005). For example, the underparts of male D. c. graueri are usually bright yellow, but in some birds these are chestnut—a feminine colour phase (female graueri underparts are heavily washed with chestnut of varying intensity). The yellow underparts of male D. c. ansorgei are sometimes washed chestnut, whilst others have a black breast patch, which is most likely a colour phase, although such birds have also been suspected to be hybrids with D. blissetti. Despite the aforementioned variation, Yellow-bellied Wattleeye has always been considered a single species.

The Chestnut Wattle-eye *D. castanea* possesses two well-differentiated subspecies, whereas Whitespotted Wattle-eye *D. tonsa* is monotypic.

The taxa blissetti, chalybea and jamesoni

This group of taxa has a fragmented distribution. Western blissetti ('Red-cheeked Wattle-eye') occurs from Sierra Leone east, reaching western Cameroon at c.09°30'E, at the foot of Mt Cameroon. Central chalybea ('Black-necked Wattle-eye') ranges from Cameroon (from Mt Kupe and the Rumpi Hills near Mt Cameroon east) to northern Gabon, with isolated populations on Bioko and in Gabela, Angola. Eastern jamesoni ('Jameson's Wattle-eye') occurs from the northern Albertine Rift and southern Sudan to a few forests in western Kenya and north-west Tanzania.

Morphological variation and sexual dimorphism are rather restricted (Figs. 3–4). Male *blissetti* has the head, upperparts, throat and upper breast glossy blackish-green, with a broad triangular chestnut patch from below the eye to the sides of throat and neck, the rest of the underparts being white; the eye-wattle is greenish-blue (Borrow & Demey 2001). The female is greyer and less glossy. Sexual plumage dimorphism is not pronounced but important in the size of the wattle, the latter being smaller in the female. The immature is duller above, with pale tawny on the

throat, which becomes darker with age. Male and female *jamesoni* are very similar to *blissetti*, but differ in having the chestnut patch smaller, restricted to the neck-sides. Male *chalybea* lacks the chestnut cheeks and has pale golden-yellow underparts (this colour changing to white after death); the eyewattle is emerald-green (Borrow & Demey 2001). The female is a duller version of the male, with smaller eye-wattles.

Arguments pro-splitting

Adult *chalybea* is rather different from the morphologically very similar, but geographically well separated *blissetti* and *jamesoni*: it has an all-black face pattern, lacking the red 'cheek', a differently-coloured eye-wattle and pale yellow, not white, underparts. Both *blissetti* and *chalybea* occur in western Cameroon, with no proof of interbreeding. Vocalisations of the three taxa differ: e.g. *jamesoni* has a song that is higher pitched with a different melodic structure to *blissetti* (see Chappuis 2000).

Arguments pro-lumping

Though *blissetti* and *chalybea* both occur in western Cameroon, they segregate altitudinally on Mt Cameroon, with *chalybea* occurring at higher elevations: they have been observed just 3 km apart (Eisentraut 1973, Languy & Njie Motombe 2003). No proof of breeding in sympatry is available.

Juveniles of *blissetti*, *chalybea* and *jamesoni* are very similar, having a common complex head pattern, which is likely a derivative—'apomorph'— character (see Hinkelmann & van den Elzen 2003 for recent use of apomorphic versus plesiomorphic characters in a case of avian taxonomy). In contrast to adult plumage, which can be an unreliable taxonomic marker (Brumfield & Brown 2001), a shared juvenile pattern is likely to be an important indication for conspecificity, and this constitutes a major argument to group the three taxa at species or superspecies level. (For the same reason—similar juvenile plumage—all populations of Yellow-bellied Wattle-eye should also be retained within a single species.)

Vocalisations vary individually. A territorial defence song is common to all taxa (Urban *et al.* 1997).

The two geographical populations of Chestnut Wattle-eye, which have always been treated as sub-









species, appear to differ as much between them in adult plumage as the populations of Yellow-bellied Wattle-eye or the taxa *blissetti*, *chalybea* and *jamesoni*. Therefore, if the allopatric populations of Yellow-bellied Wattle-eye are lumped as one species, like those of Chestnut Wattle-eye, the same should be done with the allopatric and parapatric *blissetti*, *chalybea* and *jamesoni* in order to be consistent.

Discussion

The zoogeographical, morphological and acoustic information is equivocal for the decision concerning possible conspecificity of the populations. For a definitive conclusion, detailed field studies in the contact zone, with particular attention to behaviour and vocalisations, are required. Secondly, lab-

Captions to plates on opposite page

Figure 1. Plumage variation in females of Yellow-bellied Wattle-eye *Dyaphorophyia concreta*, from top to bottom / Variation dans le plumage des femelles du Pririt à ventre doré *Dyaphorophyia concreta*, de haut en bas: *D. c. graueri*, Cameroon; *D. c. graueri*, Cameroon; *D. c. concreta*, Liberia; *D. c. ansorgei*, Angola; and *D. c. graueri*, Uganda (Guy M. Kirwan, © The Natural History Museum, Tring)

Figure 2. Plumage variation in males of Yellow-bellied Wattle-eye *Dyaphorophyia concreta*, from top to bottom / Variation dans le plumage des mâles du Pririt à ventre doré *Dyaphorophyia concreta*, de haut en bas: *D. c. graueri*, Cameroon; *D. c. concreta*, Liberia; *D. c. graueri*, Cameroon; *D. c. ansorgei*, Angola; and *D. c. graueri*, Uganda (Guy M. Kirwan, © The Natural History Museum, Tring)

Figure 3. Plumage variation in males of Blissett's Wattleeye *Dyaphorophyia blissetti*, from top to bottom / Variation dans le plumage des mâles du Pririt de Blissett *Dyaphorophyia blissetti*, de haut en bas: *D. b. chalybea*, Cameroon; *D. b. blissetti*, Liberia; and *D. b. jamesoni*, Uganda (Guy M. Kirwan, © The Natural History Museum, Tring)

Figure 4. Lateral view of the same male specimens of Blissett's Wattle-eye *Dyaphorophyia blissetti* as in Fig. 3, from left to right / Vue latérale des mêmes spécimens mâles du Pririt de Blissett *Dyaphorophyia blissetti* de la Fig. 3, de gauche à droite: *D. b. blissetti*, Liberia; *D. b. chalybea*, Cameroon; and *D. b. jamesoni*, Uganda (Guy M. Kirwan, © The Natural History Museum, Tring)

oratory studies using molecular tools are needed to supplement the results from the field.

Pending these studies, it is questionable whether one should yield to pressure to split all allopatric and parapatric taxa into species. For general use it does not really matter whether allopatric populations are treated as species or subspecies. However, although their conservation importance does not change (Knox 1994), in practice, the Red Lists for birds deal only in species.

Zink (2004) appealed for a massive reorganisation of classifications, in order that the lowest ranks, be they species or subspecies, reflect evolutionary history. He accepts the rank of subspecies for a taxon that has had an independent evolutionary history. The proper application of the subspecies concept is encouraged also by other taxonomists (see, e.g., Cicero & Johnson 2006). Helbig et al. (2002), however, advocate ranking parapatric taxa that do not hybridise as species.

It is as yet unknown what happens in the contact zone between the parapatric blissetti and chalybea. Although blissetti, chalybea and jamesoni could be considered as allospecies in a superspecies (sensu Amadon & Short 1992), under the Biological Species Concept (sensu Haffer 1997), I consider it preferable, on balance, to recognise only four taxonomic units at species level within the genus. I thus include chalybea and jamesoni as subspecies in the species D. blissetti, for which I propose the name Blissett's Wattle-eye (reflecting the current French name: Pririt de Blissett), rather than Red-cheeked Wattle-eye, as chalybea does not possess red cheeks.

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Editorial comment.—Michel Louette's remarks on the taxonomy of certain members of the genus Dyaphorophyia were produced in response to an invitation by a member of the editorial committee, in order to support his classification of these taxa in the relevant volume (11) of Handbook of the Birds of the World (Louette 2006). We very much welcome similar contributions on the taxonomy of African birds by authors of other chapters in HBW as we consider it important that such persons defend novel or revisionist systematics by also submitting such work to peer review, rather than only publishing their decisions, with little or no explanation, in the Lynx Edicions volumes. In the present instance, Louette did not have access to the forthcoming proposals regarding the recognition of species under the Biological Species Concept by Collar et al. (in prep.), for which some details have already appeared in the public domain, most notably in Collar (2006). Therein, the author uses a scoring system that grades morphological and vocal differences (major character 3, medium 2, minor 1; minimum 7 for species status, with none permitted on minor differences alone) between allopatric taxa of Asian babblers. Because of the particularly interesting case offered

by the *Dyaphorophyia* taxa studied by Louette, we invited N. J. Collar and L. D. C. Fishpool, two of the authors of the new guidelines, to conduct their own examination of these forms. Their response was as follows.

'Our 'system' requires there to be a score of 7 or more for allopatric taxa to be regarded as separate at the species level. On the basis of our scores...blissetti and chalybea come out as separate species. And that is leaving aside the question of whether they are parapatric (if they are, then a lower score is sufficient under our system to separate them). On the basis of the skins only, separation of blissetti from jamesoni is hardest to justify. scoring only 4, possibly 5. This, however, is to ignore the fact the more distinct chalybea is geographically interposed between them; what additional weighting to give such phenomena is yet to be decided. In addition, if there are vocal differences, as suggested in some literature, then the scores here would be further increased.... Overall, we are happy to continue to treat them as separate species (BirdLife currently does so).'

We urge enterprising field workers to endeavour to fill some of the relevant gaps in our knowledge of these birds, by acquiring additional vocal material and depositing this in an accessible institutional archive, such as the British Library National Sound Archive, London, (www.bl.uk/collections/sound-archive/wild.html), by studying the potential contact zone between the apparently parapatric blissetti and chalybea in western Cameroon, and by publishing their results in a journal such as Bull. ABC or other refereed publication. Pending further evidence, the ABC list will follow Dowsett & Dowsett-Lemaire (1993) and Dickinson (2003), in treating the three taxa discussed here as separate species.

Additional References

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